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Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska

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Pacific sand lance *Ammodytes hexapterus* in Kachemak Bay, Alaska, showed no sexual dimorphism in length-to-weight (gonad-free) ratio or length-at-age relationship. Most matured in their second year, males earlier in the season than females, but females (31%) attained a higher gonadosomatic index than males (21%). Sand lance spawned intertidally once each year in late September and October on fine gravel or sandy beaches soon after the seasonal peak in water temperatures. Sand lance in Cook Inlet and Prince William Sound displayed similar maturation schedules. Schools were dominated 2 : 1 by males as they approached the intertidal zone at a site where spawning has taken place for decades. Sand lance spawned vigorously in dense formations, leaving scoured pits in beach sediments. Fecundity of females (93–199 mm) was proportional to length, ranging from 1468 to 16 081 ova per female. About half of the overall spawning school fecundity was derived from age group 1 females (55% of the school by number). Spawned eggs were 1·02 mm in diameter, demersal, slightly adhesive, and deposited in the intertidal just below the waterline. Sand lance embryos developed over 67 days through periods of intertidal exposure and sub-freezing air temperatures.

Key words: sand lance; fecundity; gonadosomatic index; intertidal; Alaska.

INTRODUCTION

Sand lance *Ammodytes* spp., are zooplanktivorous, semi-demersal, schooling perciforms, ubiquitous in boreo-arctic regions of the North Atlantic and North Pacific oceans. Several species of *Ammodytes* have been described, but only *A. hexapterus* Pallas is known to occur in the north-eastern Pacific. *Ammodytes hexapterus* dominates nearshore Gulf of Alaska and Bering Sea fish communities and comprises the principal forage fish for many marine birds and mammals (Springer, 1991; Piatt & Anderson, 1996; Blackburn & Anderson, 1997). Despite their importance in the marine ecosystem, little is known about the annual life cycle of Pacific sand lance.

Sand lance are closely linked with specific benthic habitats, alternately lying buried in the substrate and swimming pelagically in well-formed schools. Hence, nearshore aggregations are typically associated with fine gravel and sandy substrates up to and including the intertidal zone (O'Connell & Fives, 1995). Sand lance are highly selective in their use of burrowing habitat (Pinto *et al.*,

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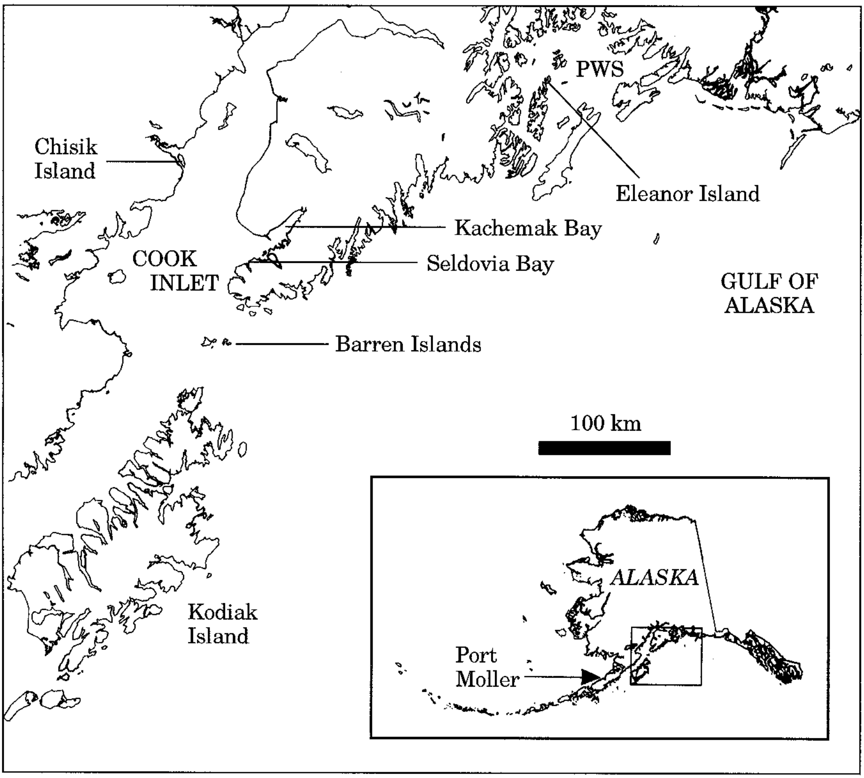

FIG. 1. Location of sand lance collections within Cook Inlet and Prince William Sound (PWS). Spawning occurred at Raby's spit (not visible at this scale), located on the west side of Seldovia Bay.

1984), but spawning habitat and substrates remain undescribed. We are aware of no year-round studies of maturation phenology for *A. hexapterus*. Most estimates of spawning phenology are based on backcalculation from the occurrence of early-stage larvae (Field, 1988). Larval surveys conducted around Kodiak suggested that sand lance spawn during February–March (Rogers *et al.*, 1979; Kendall *et al.*, 1980). McGurk & Warburton (1992) calculated that *A. hexapterus* in the Port Moller estuary (Alaska Peninsula) spawned between mid-January and late April. Captive *A. hexapterus* collected from the Strait of Juan de Fuca (Washington) also indicated late winter (March) spawning (Pinto, 1984). In contrast, the only direct observations of spawning condition *A. hexapterus* were made off Kodiak Island (Dick & Warner, 1982) and Cook Inlet (Blackburn & Anderson, 1997) during August to October.

To address this lack of information on Pacific sand lance reproductive biology, a year-round study was initiated in Kachemak Bay, Cook Inlet (Fig. 1). Local residents indicated that for decades spawning sand lance had used some beaches in this area. In this paper the first estimates of maturation phenology and fecundity for Pacific sand lance based on year-round observations are provided, and the spawning behaviour of this species in coastal waters is described.

MATERIALS AND METHODS

Kachemak Bay (Fig. 1) is near the southern tip of the Kenai Peninsula in Alaska (59°61′ N, 151°45′ W). The bay is about 38 km wide at its entrance from Cook Inlet and 62 km long. Most of the bay is relatively shallow, ranging from *c.* 35 to 90 m, with greater depths on the southern side. Most water entering the bay originates from the Gulf of Alaska, passing north of the Barren Islands (Burbank, 1977).

Sand lance were collected at many beaches throughout Kachemak Bay, but spawning was observed only at one site in Seldovia Bay (Raby's spit; 59°41′ N, 151°72′ W) at the southern entrance to Kachemak Bay. Adult sand lance were also collected during summer at Chisik Island (60°14′ N, 152°59′ W) and from Eleanor Island in central Prince William Sound (60°53′ N, 147°60′ W; Fig. 1).

Water temperatures were measured at 10-min intervals with temperature loggers (Optic StowAway version 2·02, Onset Computer Corporation) placed at 3 m depth below low water (0 m) on the south side of Kachemak Bay (permanent placement) and at Raby's Spit (only during spawning/incubation period of 1996). Air temperatures were collected in Homer by the Alaska Climate Center.

Fish were collected primarily with beach seines or by digging in intertidal substrates. Knotless seine nets were 44 m long and had 4-m deep, 3-mm nylon stretch mesh (sm) in the middle 15·3 m, tapering to 2·3 m deep with 13-mm sm wings. The net was set parallel to shore at a distance of 25 m as described by Caillet *et al.* (1986). Samples were collected about every 2 weeks from May to September and once per month through the winter during 1996 and 1997. Spawning schools were caught by setting the beach seine tangentially to the beach and closing the open end when sand lance swam into the net. About once a month, sand lance were collected by digging in exposed intertidal substrates during negative tides. No samples were collected in January.

Approximately 150 000 sand lance were caught in Kachemak Bay during 1996 and 1997, but only 19 000 of these were adults. A sub-sample of 3189 adults was analysed for age and sexual status. No adults were caught in seines during winter (November–March), these fish being found only in intertidal sediments. Sub-sampled sand lance were measured immediately (fork length in mm), blotted dry, weighed ($\pm$ 0·01 g), bagged individually, and frozen. Gonads were excised from partially thawed individuals to prevent rupturing, particularly in later developmental stages. Gonads were identified as ovaries or testes using a dissecting microscope, weighed ($\pm$ 0·001 g), and further classified as: stage 0, immature; stage I, resting (based on Nelson & Ross, 1991); stage II, developing; stage III, ripe; stage IV, running; stage V, spent; and stage VI, recovering (based on Macer, 1966).

Fecundity was calculated using stratified (by 5-mm size classes from 90 to 200 mm) samples of stage II ovaries (n=51) collected in August and September. Ovaries were removed and preserved (hardened) in 5% formalin. Before counting, ovaries were placed in small tubes and shaken vigorously with boiling water to free eggs from ovarian tissue. All eggs from both ovaries were counted individually on a partitioned Petri dish under a dissecting microscope. Samples of 150 eggs from ripe (stage III) females (n=30) were also collected. Spawned eggs were collected from a spawning pit on Raby's Spit (12 October 1996: n=100), and on subsequent visits to the spawning site (24 October, 25 November and 9 December 1996; n=78). These were kept moist in sea water to prevent desiccation and analysed immediately. Eggs were measured using an ocular micrometer at 40 × magnification. Embryo development in spawned eggs was classified into six stages as described by Smigielski *et al.* (1984).

A sub-sample (n=2800) of sand lance collected in Kachemak Bay was aged and all fish from Chisik Island and Prince William Sound. Sagital otoliths were removed from the saculus after making a transverse incision behind the skull. Fibrous material was removed from otoliths; they were then cleared and bonded to microscope slides using crystalbond thermal resin. Ages on two separate occasions were determined using the methodology of Macer (1966) and Scott (1973). Otoliths with poorly defined annuli that could not be confirmed using the second otolith, or where readings were inconsistent were omitted from the dataset (n=4). Age designations are based on a 1 January hatch date with first year fish designated as age 0 and second year fish as age 1, up to seventh year fish as age 6.

About 3 kg of substratum containing spawned eggs were collected from each of three spawning sites on Raby's Spit. Samples were dried at 65° C until no change in mass was observed. Each sample was sieved through 16-mm, 8-mm, 4-mm, 2-mm, 1-mm, 0·5-mm, 0·25-mm, 0·125-mm, and 0·063-mm sieves. Per cent mass of substratum retained by each sieve was calculated. Particle sizes were classified according to the Wentworth scale in φ units, where $\varphi = -\log_2$ diameter (mm). Median particle diameter corresponded to the 50% mark on the cumulative curve using a probability transformed y-axis (Brown & McLachlan, 1990).

A modified gonadosomatic index (I_G) was used to quantify sexual maturity on individuals of stages I–VI. All immature (stage 0) fish were omitted from this analysis. The index was calculated as: I_G=(gonad weight/gonad-free body weight) × 100 (Nikolsky, 1963).

To compare the length/weight relationships between sexes, differences in slope and Y-intercept of linear regressions using the Chow test were tested for (Salvanes & Stockley, 1996). Mann–Whitney rank sum tests were used to evaluate differences between length at age for the different sexes and between different groups of I_G values. A χ^2 test was used to assess deviation from a 50 : 50 sex ratio.

RESULTS

PHYSICAL ENVIRONMENT

Sea surface temperatures (SST) in Kachemak Bay during 1996 increased steadily from <2° C in March, plateaued at *c.* 11° C in August, and then after a mid-September peak of 12° C, declined steadily to *c.* 2° C in January 1997. Temperatures in 1997 followed a similar pattern with a slightly higher peak temperature of *c.* 13° C in August (Fig. 2). No difference between SSTs in Kachemak Bay and those at the spawning site in Seldovia Bay were observed.

Air temperatures increased steadily from a low in January, and by April were generally above freezing. Air temperatures were usually highest in August, and declined rapidly during September (Fig. 2). Beginning in October, sub-freezing temperatures were common and during most of November and December, temperatures never rose above freezing.

REPRODUCTIVE CHARACTERISTICS

Male and female lengths-at-age (Fig. 3) did not differ significantly for any age prior to gonadal development (May/June), during sexual maturation (July/August), or at spawning (September/October; Mann–Whitney rank sum test; all $P>0{\cdot}05$). Chow tests indicated no significant differences between male and female length/somatic weight relationships during pre-gonad development, gonad development, or at spawning stages (Fig. 4; $F^*=0{\cdot}851$, $P>0{\cdot}05$; $F^*=0{\cdot}000$, $P>0{\cdot}05$; $F^*=0{\cdot}067$, $P>0{\cdot}05$, respectively).

No age 0 fish (n=419) showed signs of developing gonads, although 11 fish (3%) had passed from the stage 0 to stage I phase in October. Gonads of some of the age 1 through age 4 fish did not appear to develop and remained at the immature, stage 0 phase (19% of 1310, 3% of 697, 0·3% of 287, 2% of 62, respectively). The smallest ripe male and female fish were age 1 (88 mm and 113 mm, respectively). The oldest maturing fish were a male and female of age 6 (163 mm and 173 mm, respectively). In September, most age 1 sand lance were developing or ripe (72%, n=234), and the proportion increased during spawning

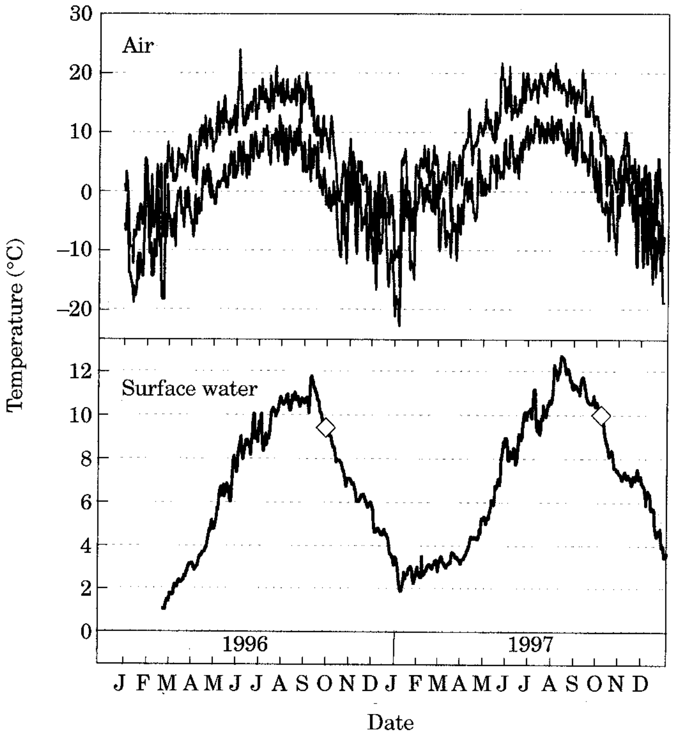

FIG. 2. Seasonal variation in maximum and minimum air temperatures and sea surface temperatures (SSTs) at Kachemak Bay in 1996 and 1997. Diamonds on SST plots indicate onset of sand lance spawning.

in October (97%, n=230). Some of these fish (15%) were also spent. These results indicate that sand lance mature at an age of about 21 months. Age 1 (50%) and age 2 (31%) sand lance dominated spawning schools. Ages 3, 4, 5 and 6 made up 14, 4, 1 and <1%, respectively, of the overall school composition.

From February to May, most sand lance were in the resting phase, and a few fish were still recovering from spawning (Table I). Gonadal recrudescence began in June and July, when a small proportion (6–9%) of fish displayed developing gonads. Gonadal development increased rapidly (Fig. 5) in August as sea surface temperature reached maximal levels (Fig. 2). Spawning-condition gonads developed as SSTs declined from seasonal peaks and spawning occurred when these SSTs reached *c.* 10° C. Gonadosomatic indices indicated that males developed earlier than females, but ultimately attained a lower index at spawning (21% males, 31% females). I_Gs differed significantly among sexes in both 1996 and 1997 (Mann–Whitney rank sum tests; all P<0·01). Maximum I_G values for individual males and females were 47 and 55%, respectively. Overall I_G values for males and females from spawning schools (Table II) were similar in 1996 and 1997, with no significant difference detected for either sex between years (Mann–Whitney rank sum tests; P>0·5). By the end of November, 67% of sand lance collected (n=24) were in postspawning condition (spent, recovering, or resting). No fish in spawning condition were found after this time (Table I). All

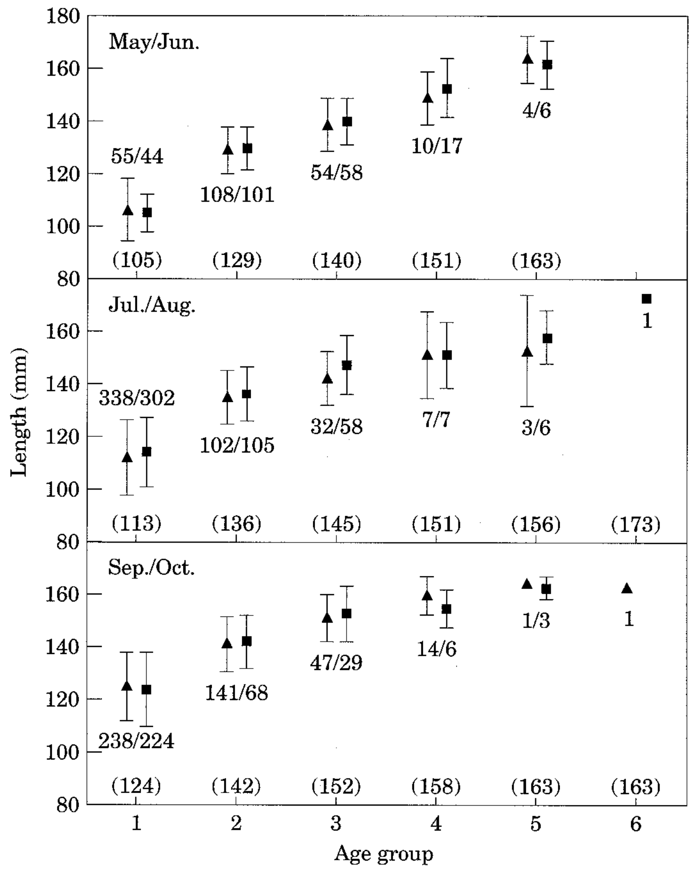

FIG. 3. Lengths-at-age (± 1 S.D.) of adult male (▲) and female (■) sand lance collected before gonad development (May and June), during sexual maturation (July and August), and while ripe and spawning (September and October) in Kachemak Bay. Numbers are samples sizes (M/F) and numbers in parentheses are overall mean lengths for sexes combined.

sizes of adult sand lance were grouped for analysis based on no significant relationship existing between I_G and body length of ripe fish collected in October (Fig. 6).

Indices of maturity revealed (Table III) that fish collected from Eleanor and Chisik Islands were maturing at time of capture (July and August, respectively). Based on a mean resting I_G (calculated from stage I fish collected during April through June from Kachemak Bay) of 0·46, sand lance from Chisik and Eleanor islands displayed significant gonad recrudescence over I_Gs observed at resting (Mann–Whitney rank sum tests; all P<0·01). These results were similar to those found for the Kachemak Bay population (Table I, Fig. 5).

During the resting and developing stages (stages I and II) in spring and summer, sex ratios were relatively even. During the spawning period however, ripe and spawning males predominated (Table IV). Males were the predominant sex in all age classes (with the exception of age class 5 in which only three fish were collected) during this period.

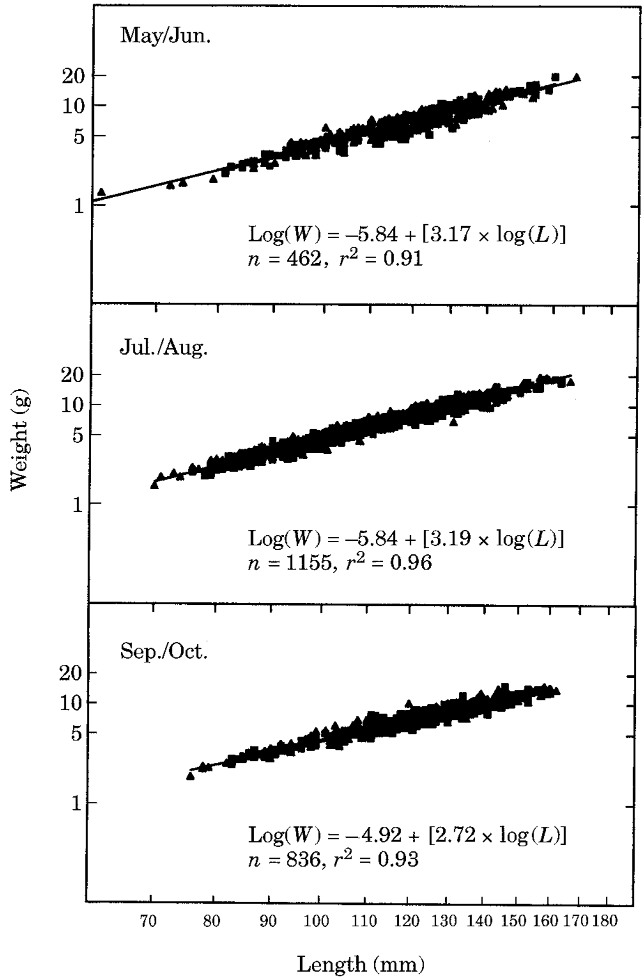

FIG. 4. Regression plots of length against gonad-free body weight (log transformed data) for male (▲) and female (■) sand lance. Sand lance were collected before gonad development (May and June; n=236 male, 226 female), during development (July and August; n=580 male, 575 female), and while ripe and spawning (September and October; n=475 male, 361 female). Regression equations are for sexes combined.

Fecundity ranged from 1468 to 16 081 ova per female for sand lance ranging from 93 to 199 mm L_F (Fig. 7). Fecundity was correlated significantly with body length (P<0·01). About half of the overall spawning school fecundity was derived from age group 1 fish, which made up 55% of the school by number (Table V). Ages 1–3 accounted for 95% of the total fecundity. Ova diameter exhibited a unimodal distribution in each of the 30 females investigated, and overall (Fig. 8). Each egg contained typically a single bright yellow oil globule (in two females about 5% of ova contained two oil globules).

SPAWNING HABITAT AND TIMING

Spawning occurred in a shallow open bay on the southern, sheltered side of Raby's spit, within 100 m of routinely used sand lance burrowing habitat. Local

TABLE I. Percentage of *Ammodytes hexapterus* classified into maturity stages by month for fish collected in Kachemak Bay

Month	Sex	Maturity stage						Total no.
		I	II	III	IV	V	VI	
Feb.	Male	95	—	—	—	—	5	21
	Female	75	—	—	—	—	25	12
Mar.	Male	100	—	—	—	—	—	8
	Female	100	—	—	—	—	—	8
Apr.	Male	92	—	—	—	—	8	24
	Female	95	—	—	—	—	5	21
May	Male	100	—	—	—	—	—	69
	Female	99	—	—	—	—	1	81
Jun.	Male	93	7	—	—	—	—	173
	Female	93	7	—	—	—	—	160
Jul.	Male	91	9	—	—	—	—	210
	Female	94	6	—	—	—	—	239
Aug.	Male	39	57	4	—	—	—	301
	Female	59	41	—	—	—	—	287
Sept.	Male	14	45	39	2	—	—	167
	Female	26	67	7	—	—	—	163
Oct.	Male	1	7	44	41	7	—	310
	Female	1	4	47	43	5	—	195
Nov.	Male	20	—	27	27	—	27	15
	Female	—	—	11	11	22	56	9
Dec.	Male	—	—	—	—	—	100	1
	Female	—	—	—	—	—	100	2

Maturity stages: I, resting; II, developing; III, ripe; IV, running; V, spent; VI, recovering.

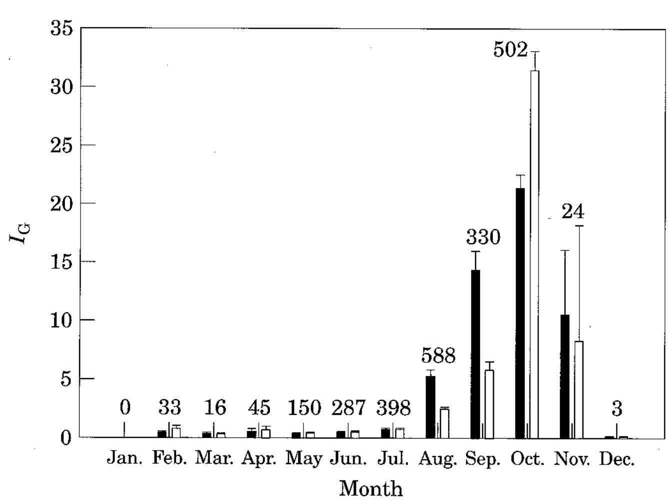

FIG. 5. Seasonal changes in male (■) and female (□) I_Gs ($\pm$95% CI) for sand lance collected in Kachemak Bay between May 1996 and October 1997. Numbers are sample sizes for each month.

TABLE II. Mean I_G ($\pm$95% CI) for male and female sand lance collected from spawning schools in Seldovia Bay

	1996	1997
Male	21·12 ± 1·65 (141)	21·57 ± 1·59 (164)
Female	31·27 ± 2·66 (89)	31·81 ± 2·09 (103)

Numbers in parentheses are sample sizes.

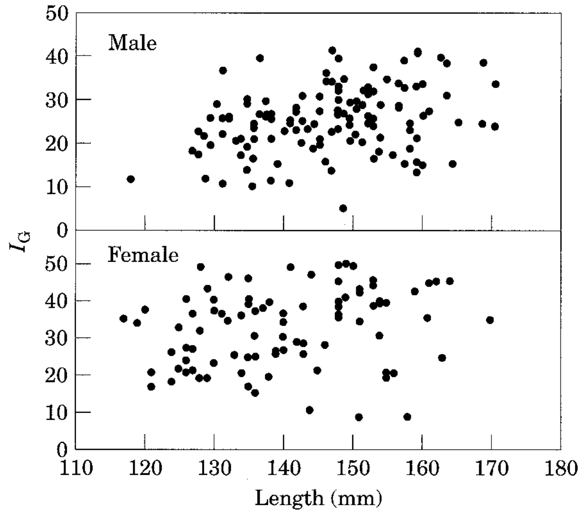

FIG. 6. Scatter plot of male (n=131) and female (n=91) I_Gs against body length for ripe (stage III) sand lance collected from spawning schools in Kachemak Bay during 1996 and 1997.

TABLE III. Comparison of maturation status at two other collection areas in southcentral Alaska

Location	Dates collected	Sex	n	Stage	I_G ($\pm$95% CI)
Chisik Island	August 1996/97	M	22	I–III	4·69 ± 1·60
		F	23	I–II	2·81 ± 0·76
		Overall	45	I–III	3·64 ± 1·06
Eleanor Island	July 1997	M	18	I–II	5·81 ± 1·32
		F	24	I–II	3·11 ± 0·53
		Overall	42	I–II	4·27 ± 0·75

residents indicated that sand lance (local name: needlefish) had spawned at this site during the month of October for at least the past 20 years. No spawning was observed on the outer exposed side of the spit in 1996 or 1997. The substrate of the spawning area consisted of coarse sand and gravel (Fig. 9) of which about 20% was shell fragments.

TABLE IV. Sex ratios of sand lance collected in Kachemak Bay at different maturity stages during 1996 and 1997

Stage	Males : Females	n	χ^2	P
0	1·3 : 1·0	350	6·6	NS
I	1·0 : 1·1	1319	5·5	NS
II	1·1 : 1·0	563	2·7	NS
III	2·1 : 1·0	321	38·4	$P<0·001$
IV	1·6 : 1·0	218	11·5	$P<0·001$
V	1·9 : 1·0	35	3·5	NS
VI	1·0 : 1·5	20	0·8	NS

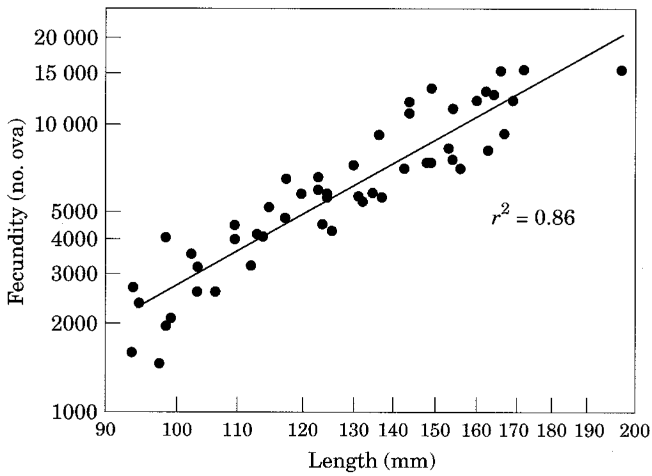

FIG. 7. Regression of fecundity on body length (log transformed data) for pre-spawning (stage II) female sand lance collected from Kachemak Bay (n=51, r^2=0·86, P<0·01; log fecundity= − 2·54+(2·99 × log length).

During 1996, sand lance were observed spawning first at 1845 hours on 30 September (1·5 h after high tide, 3 days after spring tides, and 3 days prior to the next neap tide) when SSTs were 9·4° C. Initially, the laterally compressed schools (about 1–8 m in length and up to 1 m across) of adult sand lance were observed at high tide moving back and forth along the length of the beach, within 5 m of shore, and in <1 m of water. Spawning was preceded immediately by sand lance moving back and forth along a 20-m stretch of beach (where all spawning was observed); then the school moved to the tide line and compressed into a tight spherical formation just above the bottom (with the fish moving rapidly within this formation). Milt was observed in the water soon after the school adopted this formation. Again, sand lance were observed spawning at 1825 hours (0·5 h after high tide) on 1 October, at 1830 hours [2·5 h after low tide (neap)] on 5 October, and at 0820 hours (2·5 h before high tide) on 6 October. Demersal eggs were found intertidally in shallow (<50 mm) depressions (pits) up to 0·4 m in diameter from c. 2 to 5 m above the low tide line. The pits were

TABLE V. Per cent contribution to the overall spawning school fecundity derived from females of the different age groups present in 1996 and 1997 (n=165)

Age group	% Total fish	% Total fecundity
0	0	0
1	55	48
2	26	28
3	15	19
4	3	4
5	1	1

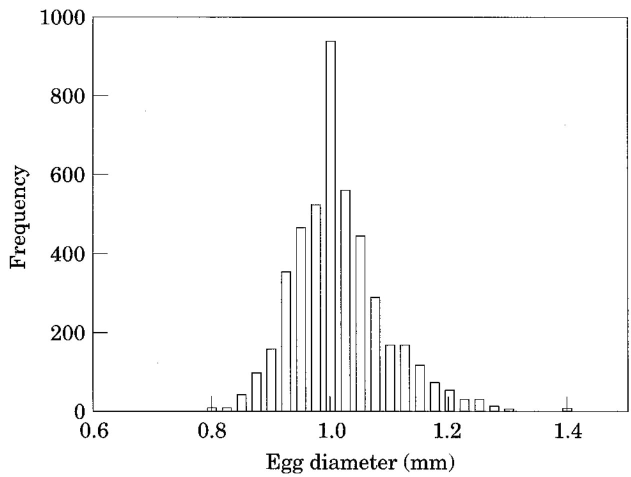

FIG. 8. Size distribution of eggs found in ovaries of 30 ripe female sand lance collected from spawning schools in Kachemak Bay during 1996 and 1997 (n=4500, mean=1·01 mm, S.D.=0·08 mm).

formed at the time of spawning by sand lance as they schooled near the bottom. Sand lance continued to spawn in these shallows, and new pits containing eggs were observed until 12 November (spring tide). During morning low tides, periodically found egg-filled pits were observed that had not been noted the previous evening, indicating that sand lance also spawn at night.

In 1997, spawning was observed first during the neap tide series on 8 October at 1600 hours (2·5 h after low tide) when SSTs were c. 10·0° C. Spawning was observed again on 9 October from 1700 to 2000 hours (mid-flood tide), 10 October at 0830 hours (1·5 h before high tide), and 11 October at 0900 hours (high tide). High winds and snow prevented observations after this, although no spawning pits were observed on any subsequent low tides. After spawning, adult sand lance were not observed swimming in the nearshore and they were not caught in beach seines until the following spring.

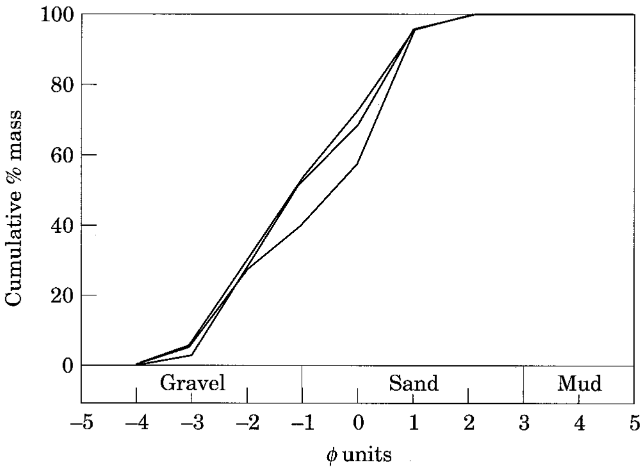

FIG. 9. Graphical representation of sand lance spawning substrate in Seldovia Bay (median particle diameter=1·9 mm). φ units= $-\log_2$ particle diameter (mm).

Sand lance eggs are cryptic and blend in well with small fragments of shell and gravel. This prevented us from making an accurate assessment of egg distribution over the entire beach. Eggs were observed on the sand surface of spawning pits at a density of up to 7 cm^{-2} and within the substratum to a depth of about 30 mm. Eggs were demersal, slightly adhesive, translucent, and almost spherical in shape (mean diameter 1·02 mm, S.D.=0·08 mm, n=100). Some eggs were adhered to sand grains or each other, but many others were found individually and unattached within the gravel.

Stage 1 eggs (<2 days old; Smigielski *et al.*, 1984) were collected on 12 October 1996 from a freshly formed spawning pit. An incomplete blastodermal cap characterized these eggs. Yolk cloudiness was not observed at this or subsequent stages. At the same pit on 24 October, eggs were at stage 3 and no blastodermal cap was evident. By 25 November, egg density at this pit had declined dramatically, and only nine eggs were observed. Only one of these nine eggs was adhered to the lightly frozen gravel particles. Each of the nine eggs contained a stage 5 embryo between 3·75 and 3·8 mm in length. Eyes were pigmented (0·18 mm diameter), myomeres were visible along most of the embryo's length, a beating heart was observed, and a developing alimentary canal was visible. On 9 December a final sample of three eggs was found at this spawning pit. All three eggs contained a stage 6 embryo which exhibited convulsive movements every 10–15 s. Assuming the eggs from this spawning pit were all part of the 12 October spawning, development over the observed 58 days (until 9 December, when stage 6 embryos were observed) occurred at an average sea and air temperature of 6·4 and −2·5° C, respectively.

DISCUSSION

Second-year spawning is common among other species of sand lance, occurring in *A. personatus* Girard (Kitaguchi, 1979), *A. americanus* DeKay

(Richards, 1982), and *A. tobianus* L. (O'Connell & Fives, 1995). In contrast, *A. dubius* Reinhardt (Scott, 1968; Winters, 1983) and *A. marinus* Raitt (Reay, 1970) can mature as second-year fish, but often mature at later ages. In our study, only a single age group 0 fish (immature) was observed within the spawning schools, although exclusively age 0 schools were caught elsewhere in the bay at the same time. The maximum lifespan for *A. hexapterus* was 7 years, which is also the upper age found for *A. tobianus* (O'Connell & Fives, 1995). For fish populations such as those studied here, wherein a single cohort at age 1 contributes 50% of the population fecundity, any large variations in recruitment are, in turn, likely to have large and immediate effects on population size.

Gonadal development was slow initially and differed between the sexes. No sexual dimorphism was observed for mature sand lance, either in their length-to-weight ratios or length-at-age relationship. Therefore we can attribute gender differences in the I_G to variable rates of gonadal development independent of differences in body size between sexes. Gonads matured rapidly in August as adult sand lance spent less time in the pelagic zone (Robards *et al.*, unpubl. data). During August and September, mean I_Gs for males were higher, indicating that males matured more quickly and earlier during the reproductive season. Initial maturation in *A. dubius* was also quite slow (Winters, 1983), and *A. dubius* (Nelson & Ross, 1991), *A. tobianus* (O'Connell & Fives, 1995), *A. marinus* (Reay, 1970), and *A. personatus* (Okamoto *et al.*, 1989) all display differential rates of maturation between males and females. While testes of *A. hexapterus* peaked in development earlier, eventually ovaries attained a greater relative weight. Gonad maturation time for *A. hexapterus* was comparable with that found for autumn-spawning Atlantic sand lance (*c.* 3 months). In contrast, winter- and spring-spawning Atlantic sand lance require from 5 to 7 months to reach maturity (Reay, 1970).

This data (maturity stages, I_G) indicate that *A. hexapterus* spawns only once per year in late autumn. The presence of a few recovering fish as late as May (Table I) indicates that some individuals may spawn later in the winter (as in *A. dubius*; Winters, 1983). However, we found no evidence for different spawning groups within the population, i.e. one that also spawns during the spring (as in *A. tobianus*; O'Connell & Fives, 1995). *Ammodytes hexapterus* from Chisik Island and Prince William Sound (PWS) also appear to spawn during the autumn.

Sand lance (*A. hexapterus*) spawned in Kachemak Bay during a 1–3-week period in October of 1996 and 1997. In the north-west Atlantic, *A. dubius* and *A. americanus* spawn over *c.* 3 months in late autumn and early winter (Winters, 1989). In Japan *A. personatus* spawns over a 1·5-month period (Okamoto *et al.*, 1989). Although the observations here indicated a shorter window of spawning within Kachemak Bay, spawning may occur over a longer period throughout the entire Gulf of Alaska region.

Male sand lance outnumbered females by about 2 : 1 in the nearshore zone during spawning, but not during earlier stages of development. This has also been observed for *A. marinus* (Macer, 1966; Gauld & Hutcheon, 1990). A higher ratio of males at spawning may indicate that they remain in the spawning area over a longer period [similar to capelin (*Mallotus villosus* (Müller); Templeman, 1948)]. Meanwhile, slower-developing females that are not fully mature probably remain buried in sediments until ready to spawn.

A unimodal size distribution of ova was found in the developing ovaries of Pacific sand lance. Unimodal size distributions of ova in *A. hexapterus* (Pinto, 1984), *A. dubius* (Scott, 1972), and *A. marinus* (Macer, 1966) are suggestive of single-batch, once yearly spawning in these species. Egg diameters for *A. hexapterus* in Kachemak Bay were comparable with other observations for this species [*c.* 1 mm for Murman sand lance (Andriyashev, 1954) and a mean of 1 mm for sand lance in the Pacific Northwest (Pinto, 1984; Penttila, 1995)]. Williams *et al.* (1964) and Pinto (1984) both observed that eggs contained one oil globule. However, occasionally multiple oil globules were observed here, which does occur infrequently in this genus (Garrison & Miller, 1982).

Fecundity of *A. hexapterus* from Kachemak Bay ranged from 1500 to 16 000 ova. This is similar to fecundity observed in most other sand lance species and populations: Japanese *A. hexapterus* (Hashimoto, 1984); *A. americanus* (Westin *et al.*, 1979); *A. marinus* (Macer, 1966); and *A. tobianus* (O'Connell & Fives, 1995). However, Nelson (1990) reported lower values for *A. dubius* and Hashimoto (1984) greater values for *A. personatus*.

Pits formed in the substrate during spawning probably result from females boring through loose gravel, and whilst doing so discharging eggs into the surrounding medium as reported for *A. tobianus* (McIntosh & Masterman, 1897). There was no significant clumping (Smigielski *et al.*, 1984) or cloudiness (Pinto, 1984) of spawned sand lance eggs as reported in laboratory studies. Although slightly adhesive, the eggs did not appear to remain on the beach in large numbers over the course of incubation. Perhaps loose adherence to gravel over time allows eggs to be dispersed by tidal action both interstitially and within the water column. Adherence of eggs to gravel and fine substrates would help prevent desiccation when they are exposed to air at low tides.

The egg development time was longer than total incubation times reported for other species of sand lance at similar water temperatures. Smigielski *et al.* (1984) and Inoue *et al.* (1967) reported incubation times of 39 days at 7°C for *A. americanus*, and 33 days at 6·2°C for *A. personatus*, respectively. Judging from a mid-stage 6 development, Kachemak Bay sand lance were at 88% development on 9 December; suggesting a 67-day total incubation period. Thus, hatching should have occurred on or around December 17. The total incubation times were similar to the 62-day incubation period reported for *A. americanus* eggs at 2°C (Smigielski *et al.*, 1984). The long incubation period observed in Kachemak Bay may have resulted from exposure of eggs to very cold air temperatures during the *c.* 12 h of intertidal exposure each day (Fig. 2). McGurk & Warburton (1992) reported comparable results for *A. hexapterus* in the Port Moller estuary on the Alaskan Peninsula (45–94 days of incubation with a hatching period of 41–63 days).

The location of deposited eggs within the intertidal has a substantial influence on development and survival rates. Similar to Taylor's (1984) finding *A. hexapterus* eggs deposited in the intertidal developed more slowly than for other sand lance species that lay eggs immersed in the sub-tidal. Increased egg survival in the intertidal compared with the sub-tidal has been attributed to lower temperatures for surf smelt *Hypomesus pretiosus* Girard (Loosanoff, 1937), and to increased oxygenation for Pacific herring *Clupea pallasi* Valenciennes (Jones, 1972).

During the spawning period, sand lance appeared to spawn with little regard for tidal stage or time of day. However, spawning may occur more frequently at high tide as evidenced by the high position of spawning pits on the beach. Penttila (1995) observed a similar vertical spread of intertidal spawning pits, i.e. within a few metres of the high water line with egg deposition in the top 30 mm of gravel.

There was no indication that sand lance moved above the high waterline as described for grunions (*Leuresthes* spp., Thompson, 1919) and capelin (Templeman, 1948). Reports of sand lance found above the waterline in the intertidal zone (Dick & Warner, 1982) may result from sand lance being stranded on low-angled beaches by rapidly retreating tides. Stranding may also be the result of predators (intentionally or inadvertently) herding sand lance into the shallows where they may be swept above the water line by the surf (Beston, 1928).

Spawning of *A. hexapterus* occurred on fine gravel and sandy beaches as is typical of this species (Penttila, 1995). Results of the 2-year study and long-term observations by local residents suggest that sand lance use the same sites for spawning year after year for decades. Penttila (1995) also documented repeated use of spawning sites. Perennial use of the same beaches has direct implications for the conservation of this species and for the predators that rely on sand lance. Sand lance may be particularly vulnerable to pollution of coastal areas and development of beach-front habitats. It would be useful to establish a quantitative library of beach substrates to help identify potential spawning habitat for this key species.

The study did not determine if Pacific sand lance are obligate intertidal spawners. Penttila (1995) collected sub-tidal samples in the vicinity of fresh intertidal sand lance spawning and did not find any evidence for coincident sub-tidal spawn deposition. No published references to offshore spawning by *A. hexapterus* were found, unlike for capelin that spawn intertidally as well as in deeper offshore waters (Templeman, 1948). The intertidal spawning of pelagic species such as capelin appears to be optional (Taylor, 1990). Our results corroborate with Reay (1970) who suggested sand lance spawn within their normal habitat, rather than migrating to special spawning areas. *Ammodytes tobianus* is the only other sand lance species known to spawn intertidally (McIntosh & Masterman, 1897). *Ammodytes marinus* (Reay, 1970), *A. americanus* (Westin, 1979), *A. dubius* (Winters, 1983), and *A. personatus* (Kimura *et al.*, 1992) all spawn sub-tidally in nearshore areas and/or on shallow offshore banks.

Late autumn spawning in the intertidal is unusual: eggs and larvae are exposed to harsh winter conditions leading to prolonged incubation and hatch periods. Pelagic sand lance larvae appear in late March and April (Haldorson *et al.*, 1993), well in advance of the spring phytoplankton bloom or the herbivorous copepod maximum. This is unlike many other fish larvae which occur much later (May) in approximate synchrony with maximum zooplankton densities (Haldorson *et al.*, 1993). The ecological significance of this timing is thought to be adaptive in situations where prey availability is unpredictable (Haldorson *et al.*, 1993). However, other factors of ecological significance may be (1) to utilize the full period of prey abundance, (2) to avoid inter-specific competition, and (3) to develop at a time of low predator abundance (Wright & Bailey, 1996). Hence, adaptations such as delayed and variable egg development, larval feeding before absorption of yolk sac (Yamashita & Aoyama, 1985), reduced metabolism at cold temperatures (Haldorson *et al.*, 1993), and resultant reduction in caloric requirements (Buckley *et al.*, 1984) all appear to increase the survivorship and chance of sand lance larvae being able to capitalize fully on the spring plankton bloom.

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